The changes in blood pressure after ESB of the posterior hypothalamus did not parallel those seen in heart rate (Fig. 1, C and D). Analyses of variance and subsequent Duncan's tests indicated some attenuation of blood pressure during slow sessions in animals M-1 and M-4. Stimulation of the anterior hypothalamus produced changes in blood pressure similar to those seen in heart rate (Fig. 1), and there was no attenuation of either during slow sessions. Analyses of variance and Duncan's tests indicated that the differences between stimulation and nonstimulation were greater in slow conditions than in (i) speed and control conditions for M-2, (ii) control for M-3, and (iii) speed for M-4. Thus no attenuation of blood pressure occurred during slow conditions.

The results of striatal stimulation were similar to those seen after posterior hypothalamic stimulation. This was true for blood pressure as well as heart rate. Thus, the change in heart rate was attenuated during slow but not during speeded or control sessions, and blood pressure did not change across conditions. The effect on heart rate of stimulating the subthalamic nucleus was similar to that of stimulating the anterior hypothalamus. Strong effects were seen on heart rate, and the animals were not able to attenuate these effects during slowing.

The data show that the ability of an animal to significantly attenuate its cardiovascular responses to stimulation of sites in the striatum or posterior hypothalamus was selective to the modality on which a negative reinforcement contingency was placed—heart rate but not blood pressure. The attenuation was not the result of threshold changes after repeated stimulation, since (i) counterbalancing controlled for order effects, and (ii) analysis of variance of changes in heart rate during the first stimulus segment in the control sessions with the last stimulus segment for each brain area showed neither segment differences nor segment differences as function of the brain area in any animal.

Smith *et al.* (*10*) have shown that lesions in areas in the baboon corresponding to our anterior hypothalamic sites create deficits in an animal's ability to generate a conditioned emotional response (a change in heart rate or blood pressure in response to a stimulus paired with an electric shock). It is possible in our experiments that affective responses elicited by stimulation in these areas override the reinforcement strength of shock avoidance. The striatal or posterior hypothalamic stimulations were overridden because they are associated with cardiovascular effects only. Cardiovascular efferents to the posterior hypothalamus may involve only outputs from the anterior hypothalamus (*10, 11*). The subthalamic nucleus is a complex area that mediates motor as well as cardiovascular functions (*12*) and that may receive selective input from the anterior hypothalamus and striatum. One conclusion is clear. Central nervous and autonomic interactions in the unanesthetized animal vary and can be modified by training. Differences in response to ESB suggest that a variety of mechanisms operate within the brain to mediate plasticity such as that seen here. The heart rate responses, even in the face of ESB, can differ as a function of environmental contingencies and the demands made on the animal.

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6. Stereotaxic coordinates relative to bregma were (i) striatum: 14 to 16 mm anterior, 1.5 to 4.0 mm lateral; (ii) anterior hypothalamus: 13.5 mm anterior, 1.5 to 3.0 mm lateral; (iii) posterior hypothalamus: 8.5 to 10.0 mm anterior, 1.5 to 4.5 mm lateral; and (iv) subthalamic nucleus: 7.0 mm anterior, 3.0 to 4.5 mm lateral [R. S. Snider and J. C. Lee, *Stereotaxic Atlas of the Monkey Brain* (Univ. of Chicago Press, Chicago, 1965)].
7. A stimulator (Grass model S48) was used in conjunction with a Grass stimulus isolation unit (Grass model SIU-5) and a constant current unit (Grass). The intensities used were sufficient to raise heart rate or blood pressure by 20 percent and ranged from 50 to 1000 μA.
8. Histologies were carried out at the experimental pathology laboratory, Herndon, Virginia, according to their standard protocol. Striatal penetrations included the caudate nucleus, the lenticular nucleus, and the lateral portion of the area tegmentum. The anterior hypothalamus included the dorsomedial anterior hypothalamus and the anterior lateral hypothalamus. The posterior hypothalamus included the mammillary bodies and the posterior dorsomedial hypothalamus. The subthalamic nucleus included the subthalamic nucleus and the parafascicular nucleus.
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13. We thank V. Hayhurst, J. Whitaker, R. Quilter, and C. Dodd for excellent technical assistance.

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Pigeons with a Deficient Sun Compass Use the Magnetic Compass

Abstract. *Homing pigeons that had never seen the sun before noon could not use the sun compass in the morning; nevertheless they were homeward oriented. When such birds carried magnets, however, they were disoriented, suggesting they were using a magnetic compass. These findings indicate that the magnetic compass is available to pigeons whether or not the sun compass has been established and that the magnetic compass is apparently the first source of compass information.*

Experiments with birds whose internal clock was phase-shifted demonstrate that the sun compass is used by homing pigeons whenever the sun is visible (*1*). This compass system is learned rather than innate (*2*), and we therefore studied that learning process. Tests indicated that knowledge only of the descending part of the sun's arc was not sufficient to establish the sun compass for the entire day. Young pigeons that had observed the sun only in the afternoon and that were tested in their subjective morning did not react to the shifting of their internal clock but departed homeward oriented (*3*).

These findings led to a question about how such birds orient if they are not able to use the sun compass. One possibility is that they rely on the earth's magnetic field for compass information (*4, 5*). If this were so, then attaching magnets to them might cause disorientation. A group of experimental pigeons was prevented from seeing the sun in the morning; they grew up in a light-tight room in a natural photoperiod and were allowed to enter their aviary or fly around their loft only in the afternoon after the culmination of the sun. Control pigeons grew up in an identical room, but these birds had access to their aviary all day and were released for exercise flights at various times of day. Both groups had a series of training flights in which flocks were released, up to 30 km in the cardi-

Table 1. The homing performance of four groups of pigeons.

Group	N (number of birds released)	Bearings	Mean vector		P (Rayleigh test)	Median vanishing interval (seconds)	Returns			Median homing speed (km/hour)
			Direction	Length			Same day	Later	Percent	
Controls	74	57	356°	0.70	<.001	172	70	3	99	16.6
Controls with magnets	61	57	353°	0.74	<.001	187	55	4	97	19.4
Experimentals	72	54	353°	0.54	<.001	242	62	4	92	11.3
Experimentals with magnets	62	54	13°	0.18	>.05*	202	49	6	89	10.3

*Not significant.

nal compass directions. At the time of the tests, the birds were about 4 months old and had ample flying experience, but the experimental birds had been released in the afternoon only.

The critical tests took place on sunny days early in the morning, at a time of day when the experimental pigeons had never been outside before. Half of the experimentals and half of the control birds were released carrying small bar magnets. These magnets (2.6 by 0.6 by 0.3 cm and about 4 g) had a pole strength of approximately 85 centimeter-gram-seconds (*6*); they were fixed on the pigeon's back between the wings with veterinary branding cement, and their north poles pointed toward the pigeons' heads. Birds of all four treatments were released alternately so that all groups were exposed equally to any temporally changing environmental conditions (*7*). Each bird was tossed singly from the hand and watched by two observers with binoculars until it vanished from sight; its last bearing was recorded to the nearest 5°, and the interval between release and vanishing was recorded with a stop watch. The mean vector of each set of bearings was calculated by vector analysis, and the bearings from different test sites were combined by setting the home direction to 360°. The data were tested for significant directional tendencies by the Rayleigh test, and two samples were tested for differences in scatter by the Mardia Watson Wheeler test (*8*).

Figure 1 shows the departure bearings of the four groups. The control birds without magnets (*9*) were homeward oriented (Fig. 1A) as was the experimental group without magnets (Fig. 1B); although the experimental birds had never before been outside their loft in the morning, they were able to orient. Magnets did not impair the orientation of the control birds, which were accustomed to flying in the morning (Fig. 1C). But the experimentals with magnets were not oriented (Fig. 1D); their departure bearings were significantly more scattered than those of the other three groups ($P < .001$ for both groups of controls, and $P < .01$ for the experimentals without magnets, Mardia test) (*10, 11*) (Table 1).

The controls carrying magnets were presumably using their sun compass. The experimental birds, which had never seen the sun in the morning, apparently could not do this; their orientation was impaired by the magnets, suggesting that they relied on magnetic information. The simplest explanation is that these birds use a magnetic compass and that the magnets caused disorientation similar to that of experienced birds in overcast conditions (*5*) by preventing the birds from localizing their home direction (*12*).

Thus our findings show that the magnetic compass is available to birds whether or not a sun compass has been established. This is in agreement with other findings (*13*) that indicate that the magnetic compass is normally used by very young birds before the sun compass is established. Our results suggest that the magnetic field is the first source of compass information in birds, preceding the use of the sun, which is the preferred compass of experienced birds.

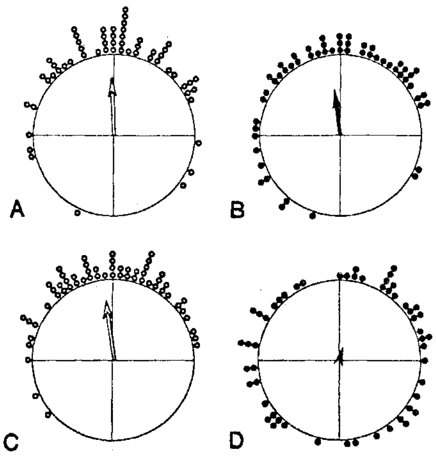

Fig. 1. When released early in the morning, the control pigeons (A) were oriented, and so were the experimentals that had never been outside their loft at that time of the day (B). Magnets did not affect the orientation of the controls (C), but the experimentals with magnets were no longer oriented (D). The vanishing bearings of individual birds are represented by the dots outside the circles, and the mean vectors are shown as arrows whose lengths are drawn proportional to the circle of radius 1.

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6. The magnets were supplied by W. T. Keeton, Cornell University, Ithaca, N.Y., and were of the same type he used in his experiments (*5*).
7. The following release sites were used: home direction 203°, distance 13.3 km (twice); 242°, 21.3 km; 198°, 28.3 km (twice); and 192°, 40.1 km.
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9. We did not use brass bars because the mere fixing of a weight on the bird's back does not affect the orientation behavior (*5*) and, in our tests, any possible unspecific effect of the magnets would have interfered with the control birds that were carrying magnets as well.
10. Altogether, there were six releases: one in 1978, two in 1979, and three in 1980. The orientations of the controls, the controls carrying magnets, and the untreated experimentals were statistically significant ($P < .05$, Rayleigh test) in five of the six releases, whereas the experimentals with magnets did not show a significant directional tendency in any of these releases.
11. The vanishing intervals of the two groups of controls did not show a statistically significant difference ($P < .05$, Mann-Whitney test); the experimentals without magnets took significantly ($P < .01$) longer to vanish than both control groups. The vanishing intervals of the experimentals with magnets, however, were not significantly different from those of the other three groups. Both control groups homed significantly ($P < .01$, Mann-Whitney test) faster than the two groups of experimentals; the magnets, however, did not affect the homing speed significantly in either group. This finding, that the effect of magnets on initial orientation is far greater than

the effect on homing performance, is in agreement with similar observations by Keeton (5) in his magnet tests in overcast conditions.

12. Our results also rule out inertial navigation as suggested by J. S. Barlow [*J. Theor. Biol.* **6**, 76 (1964)], and the short vanishing intervals of the experimentals without magnets (median, 242 seconds) make a scanning of map gradients highly improbable, as discussed theoretically by H. G. Wallraff [*Das Navigationssystem der Vögel* (Oldenbourg, Munich, 1974), p. 64]; compare also W. T. Keeton [in *Advances in the Study of Behavior*, D. S. Lehrman *et al.*, Eds. (Academic Press, New York, 1974), vol. 5, pp. 47–132].
13. Keeton (5) demonstrated that inexperienced pigeons were disoriented by magnets in sunny conditions. Recent clock-shift experiments show that very young and inexperienced pigeons do not use the sun compass but are nevertheless well oriented (R. Wiltschko and W. Wiltschko, *Behav. Ecol. Sociobiol.*, in press). Together these findings suggest that the early navigational abilities include the magnetic compass.
14. All computer work for this study was carried out by the Hochschulrechenzentrum of the Universität Frankfurt a.M. We thank W. Mann, U. Kotzur, and all the other helpers who assisted in maintaining and testing the birds. Thanks are also due to C. Walcott, State University of New York at Stony Brook, for critically reading an early draft of this report and to W. T. Keeton for methodological assistance. This study was supported by the Deutsche Forschungsgemeinschaft in program SFB 45.

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Modification of the Discharge of Vagal Cardiac Neurons During Learned Heart Rate Change

Abstract. *Visually conditioned heart rate change in the pigeon has been developed as a vertebrate model system for the cellular neurophysiological analysis of associative learning. In previous studies of the "final common path," it was shown that both the vagal and sympathetic cardiac innervations contribute to this response. The present experiments indicate that, prior to any behavioral training, the visual stimulus elicits a small decrease in the discharge of vagal cardiac neurons. During conditioning, this stimulus evokes a progressively greater decrease in discharge that parallels the acquisition of the conditioned cardioacceleration. In contrast, nonassociative control animals show habituation of the initial decrease in discharge. These data confirm the involvement of the vagal cardiac innervation in conditioned heart rate change, indicate that the vagal innervation acts synergistically with the sympathetic to produce cardioacceleration, and suggest that a short-latency pathway mediates the conditioned response.*

The neuronal mechanisms of information storage remain one of the principal challenges in contemporary neurobiology. Over the past decade, however, the development of effective model systems has significantly advanced our understanding of the cellular basis of nonassociative learned behaviors. This progress has resulted largely from the exploitation of "simple" invertebrate models, but few effective systems are available for cellular analysis of associative learning or of learning in vertebrates (*1*).

Over the past 15 years we have been developing one such model that permits cellular analysis of both nonassociative and associative learning in a relatively simple vertebrate system (*2*). The associative learning is established with a conventional Pavlovian procedure in which whole-field retinal illumination (the conditioned stimulus, CS), is paired with foot shock (the unconditioned stimulus, US), to produce a learned change in heart rate (the conditioned response, CR). Behaviorally, this system is now well characterized and has many attractive properties for cellular neurophysiological analysis (*3*). For example, in the pharmacologically immobilized animal, stable conditioning develops in 30 minutes and asymptotic performance in approximately 2 hours (*4*). Moreover, considerable effort has been devoted to identifying the relevant neural circuitry, and a first approximation to a necessary pathway from the eye to the heart is now available (*2*).

As part of this effort to map the neural circuitry, we established that the CR is mediated entirely by the cardiac nerves and that both vagal and sympathetic innervations participate. Moreover, the cells of origin of this "final common path" have been localized and criteria established for their electrophysiological identification in the behaving animal (*5*).

We now describe the discharge characteristics of vagal cardiac neurons during CR development. The objectives of investigating these motoneurons were (i) to describe the temporal properties of the informational flow along the identified pathways, unconfounded by delays at the motor periphery, and (ii) to characterize more precisely the vagal and sympathetic contributions to conditioned heart rate change.

We studied 23 experimentally naïve white Carneaux pigeons (*Columba livia*), ranging in age from 2 to 6 months and weighing 450 to 650 g. Under pentobarbital anesthesia, the posterior cerebellum was removed to expose the floor of the fourth ventricle. Five to ten days later cellular neurophysiological experiments were undertaken. The animals were immobilized with α-bungarotoxin (*4*), artificially ventilated, and placed in a stereotaxic apparatus in an acoustic chamber. Electrodes for monitoring the electrocardiogram and delivering the foot shock were inserted (*3*), and the left pupil was dilated and a contact lens placed over the cornea (*4*). Under lidocaine anesthesia, the midcervical, right vagus nerve was exposed and placed over a bipolar Ag-AgCl electrode for stimulation. A $4M$ NaCl micropipette (8 to 12 megohm) was advanced into the brainstem, and single vagal cardiac units were isolated and identified (*5, 6*).

After an adaptation period, either conditioning ($N = 13$) or sensitization ($N = 10$) training was initiated. For both procedures, the visual stimulus was a 50 foot-lambert (1 foot lambert = 3.4263 cd/m^2), monocular presentation of 6-second whole-field illumination; this stimulus was delivered through a fiber-optic bundle and an electronically controlled shutter (*4*). The foot shock consisted of a 500-msec train of biphasic pulses delivered at 60 Hz with a constant-current

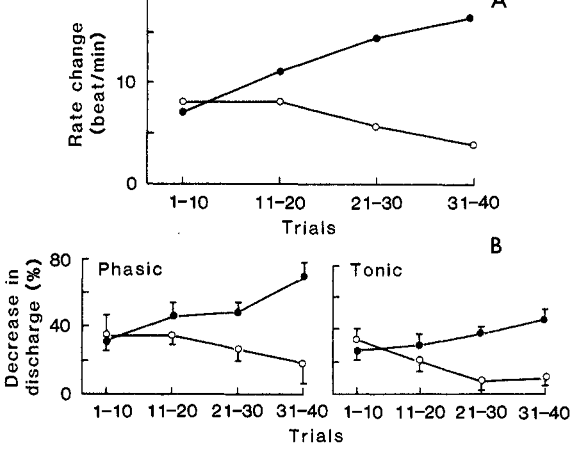

Fig. 1. (A) Mean differences between heart rates during the light and preceding control periods of birds receiving conditioning (●) ($N = 13$) or sensitization (○) ($N = 10$) procedures. Each point represents a group mean for a block of ten trials. (B) Mean discharge changes of vagal cardiac neurons during the phasic and tonic response periods during conditioning ($N = 10$) and sensitization ($N = 8$). Each point represents a group mean for a block of ten trials, and the error bars represent 1 standard error of the mean. Units were recorded from the same birds as in (A).

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